Evaluating Great Smoky Mountains National Park as a Population Source for the Wood Thrush

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Abstract: *The prevailing fragmentation paradigm predicts that large, intact forests are acting as population sources for Neotropical migrant landbirds. We used the Wood Thrush (*Hylocichla mustelina*) as a model for evaluating the role Great Smoky Mountains National Park (the largest national park in the eastern United States) may play in maintaining regional songbird populations. We estimated the annual productivity of Wood Thrushes in the park by combining observations on the birds' distribution, abundance, and productivity with estimates of habitat availability. We estimated a breeding population of approximately 10,000 nesting pairs using habitat models developed from over 2500 point-count censuses conducted across the park. Data from 426 nests monitored from 1992 to 1997 produced a daily nest survival rate of 0.96. We estimated an annual fecundity of 2.76 fledglings per breeding pair, based on a model that incorporated the re-nesting behavior of Wood Thrushes. Results indicate that the park is producing approximately 3000 surplus female young each year. Daily nest survival rates were below those reported in other studies of Wood Thrushes in large forest tracts. The relatively high productivity of 3.31 nestlings per successful nest suggests that, in the absence of predation, the park provides high-quality nesting habitat for Wood Thrushes, but that it may also support a more diverse and abundant predator community than more disturbed or less contiguous sites. The difficulties of estimating the size of continental breeding bird populations make assessing the significance of the park within a regional landscape context problematic, but our estimates suggest that, although the park is functioning as a substantial population source on a local scale, its potential to sustain regional or continental Wood Thrush populations is limited. Our findings suggest that species such as the Wood Thrush are capable of moderate levels of surplus productivity in high-quality habitat, but that extensive areas of suitable habitat outside protected areas and other public lands will be required to sustain continental breeding populations.*

Evaluación del Parque Nacional Great Smoky Mountains como una Población Fuente para el Zorzalito Americano *Hylocichla mustelina*

Resumen: *El paradigma prevaleciente sobre la fragmentación predice que bosques extensos e intactos actúan como fuentes de poblaciones de aves migratorias neotropicales. Utilizamos a* Hylocichla mustelina *como modelo para evaluar la función que juega el Parque Nacional Great Smoky Mountains (el parque nacional más grande del este de los Estados Unidos de América) en el mantenimiento de la diversidad de aves canoras en la región. Estimamos la productividad anual de* Hylocichla mustelina *en el parque combinando observaciones de distribución, abundancia y productividad, con estimaciones de calidad y disponibilidad del hábitat. Estimamos que hay aproximadamente 10,000 parejas reproductoras al aplicar modelos de hábitat basados en más de 2,500 censos realizados a través del parque. Los datos de 426 nidos, de los que se hizo un seguimiento desde 1992 hasta 1997, arrojaron un promedio de sobrevivencia diaria por nido de 0.96. Estimamos que la fecundidad estacional de* Hylocichla mustelina *es de 2,76 crías por pareja usando un modelo que incorpora segundos intentos de anidación. Los resultados indican que el parque está produciendo un excedente de alrededor de 3,000 hembras juveniles cada año. Las tasas de sobrevivencia diaria de nidos estuvieron por debajo de las tasas reportadas en otros estudios de* Hylocichla mustelina *realizados en bosques de*

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gran extensión geográfica. La productividad relativamente alta de 3.31 crías por nido exitoso sugiere que el parque provee hábitat de alta calidad para Hylocichla mustelina*, pero que también sostiene una comunidad de depredadores diversa y abundante cuando se compara con lugares más perturbados o menos contiguos. Las dificultades para estimar el tamaño de las poblaciones reproductoras de aves continentales hace que la evaluación de la importancia del parque dentro de un contexto de paisaje sea problemática, sin embargo, nuestras estimaciones sugieren que a pesar de que el parque esté funcionando como una fuente poblacional considerable a nivel local, su potencial para sostener poblaciones de* Hylocichla mustelina *a nivel regional o continental es limitado. Nuestros hallazgos sugieren que especies como* Hylocichla mustelina *son capaces de tener una productividad excedente a niveles moderados en hábitats de alta calidad, pero que se requerirán áreas extensas de hábitat propicio para la reproducción fuera de las áreas protegidas y otros terrenos públicos para proteger las poblaciones continentales.*

Introduction

Source-sink models examine how the spatial variability in population birth and death rates influences equilibrium population levels (Pulliam 1988). Forest songbirds, which are highly mobile and often rely on patchy habitats, are particularly well suited to the application of source-sink models (Villard et al. 1992; Donovan et al. 1995*a*). Pulliam's model stresses the importance of knowing the size, distribution, and productivity of population sources (patches with positive population growth rates) and population sinks (patches with negative population growth rates). The model fits well with much of the field data on forest songbird nesting success and is emerging as a popular paradigm for the effects of forest fragmentation (Robinson et al. 1995). Robinson et al.'s regional source-sink hypothesis predicts that large, intact forests act as population sources for Neotropical migratory landbirds and that small, isolated patches often serve as population sinks. Source-sink models predict that, under certain conditions, only a small fraction of a breeding population occupies source habitats (Pulliam 1988), suggesting that parks and other protected areas may be significant in sustaining populations beyond their boundaries.

We used the Wood Thrush (*Hylocichla mustelina*) as a model for evaluating the role of Great Smoky Mountains National Park (the largest national park and the largest continuous block of mature forest in the eastern United States) in sustaining the region's avifauna. Although the Wood Thrush is still a fairly common breeding species in eastern deciduous forests (Fig. 1a), continental populations tracked by the Breeding Bird Survey have shown highly significant declines averaging 1.8% annually from 1966 to 1996 (Sauer et al. 1997).

Although considerable variation in population size has been noted on smaller temporal and spatial scales (Roth et al. 1996), annual declines in Wood Thrush populations have been among the most consistent recorded, and the species has been identified as a high priority for management and monitoring in the southeastern United States (Hunter et al. 1993). Suspected causes of the decline include high rates of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) in fragmented landscapes (Robinson 1988; Hoover & Brittingham 1993; Robinson et al. 1993), higher rates of nest predation in small forest patches and fragmented landscapes (Wilcove 1985; Hoover et al. 1995; Robinson et al. 1995), and factors affecting populations on their wintering grounds (Rappole et al. 1989). Long-term studies are beginning to show that local population trends in migratory songbirds are the result of a complex mix of factors affecting mortality, emigration, and recruitment (Askins et al. 1990; Sherry & Holmes 1992; Roth & Johnson 1993; Roth et al. 1996; Weinberg & Roth 1998).

In some portions of the species' range, breeding habitats are clearly serving as population sinks in which local productivity is failing to replace losses due to mortality (Robinson 1988; Temple & Cary 1988; Robinson 1992; Robinson et al. 1995; Trine 1998). Sink habitats are becoming common in highly fragmented landscapes such as those around major urban centers (Robbins 1979) or agricultural lands (Brawn & Robinson 1996). In the Midwest, even relatively large forest tracts (1100–2200 ha) surrounded by agricultural land appear to be functioning as population sinks because of the combined effects of nest predation and cowbird parasitism (Trine 1998).

In contrast, several recent studies (Donovan et al. 1995*b*; Hoover et al. 1995; Robinson et al. 1995) have shown that rates of nest predation and cowbird parasitism on nesting Wood Thrushes are lower on larger forest tracts and less fragmented landscapes. These findings suggest that large areas of contiguous protected forest, such as Great Smoky Mountains National Park, might be functioning as population sources for forest songbirds, but the premise has never been tested empirically. Wood Thrushes are widely distributed and fairly abundant in the park, and evidence that their populations have been stable over the past 45 years (Stupka 1963; Kendeigh & Fawver 1981; Wilcove 1988; Alsop 1991; Simons et al. 1998) suggests that the park may be functioning as a population source.

Our objective was to assess the functional significance of Great Smoky Mountains National Park in sustaining Wood

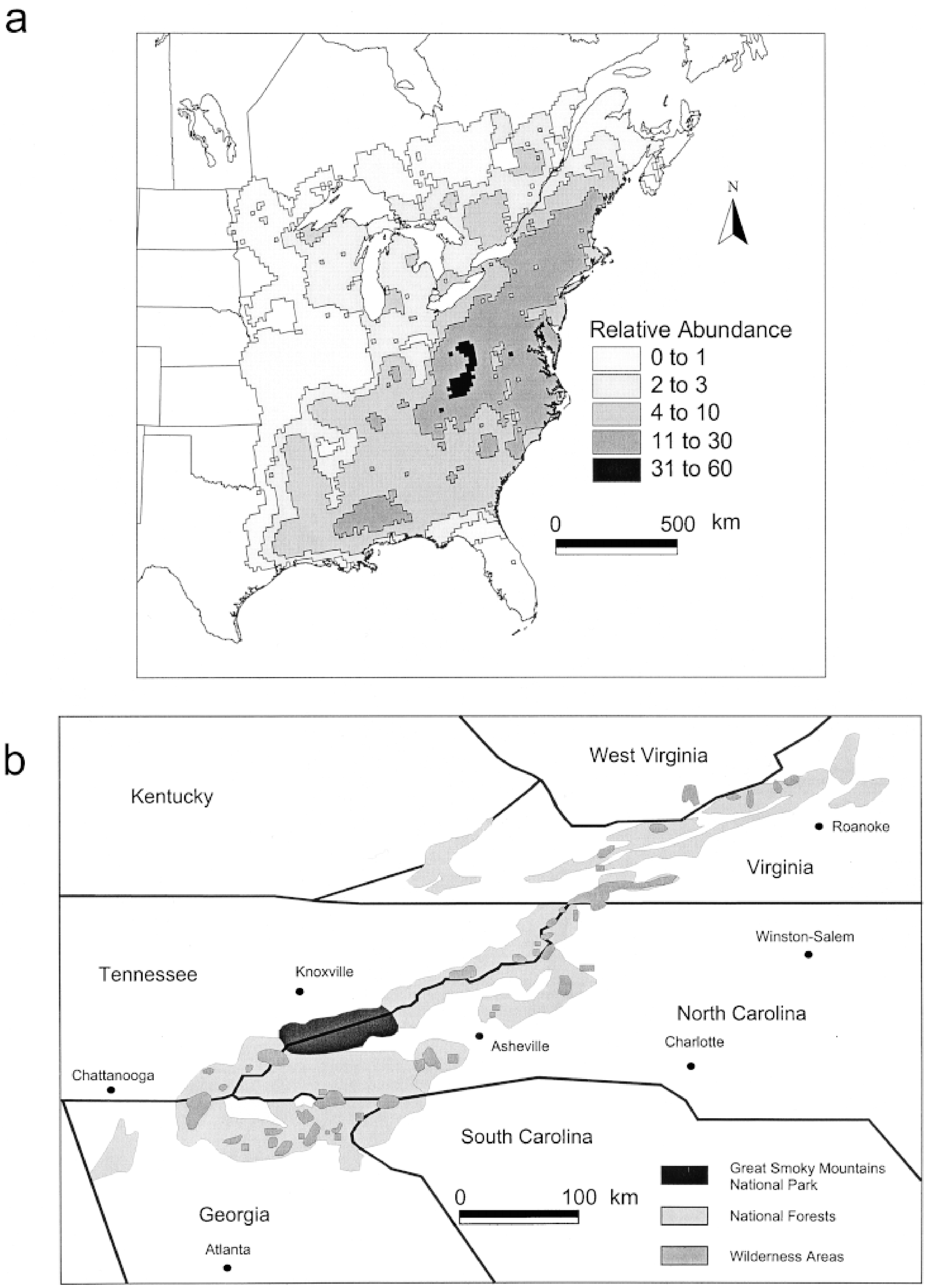

Figure 1. (a) The breeding range of the Wood Thrush and relative abundance estimates derived from the Breeding Bird Survey (Sauer et al. 1997), presented as average number of birds detected per survey route. (b) The locations of Great Smoky Mountains National Park and other public lands in the southern Appalachians.

Thrush populations on larger spatial scales. We combined estimates of adult and juvenile survival rates from the literature; field data on the birds' distribution, abundance, and nesting success in the park; a habitat model; and an annual fecundity model to generate estimates of the park's annual productivity of Wood Thrushes. We then used population estimates based on Breeding Bird Survey data to evaluate the significance of the park as a population source within both a regional and a continental context.

Methods

Study Area

Great Smoky Mountains National Park protects 205,665 ha of contiguous forest straddling the Appalachian Trail along the Tennessee–North Carolina border. A temperate climate and steep, complex topography promote broad gradients of temperature and moisture across the park's environments. These gradients produce levels of species diversity unmatched elsewhere in North America (Southern Appalachian Man and Biosphere 1996). Established in 1934, the park serves as the nucleus of the protected areas in the southern Appalachians. The more than 2 million ha of public lands in the region include a rich matrix of national forests, federally designated wilderness areas, state lands, Tennessee Valley Authority reservoirs, and National Park Service lands, comprising the largest protected forested landscape in the eastern United States (Fig. 1b).

MacKenzie (1993) used 90 m–resolution Landsat imagery and Whittaker's (1956) classification based on 15 major plant community types to develop a vegetation map of Great Smoky Mountains National Park. Seven community types that occur along a wet-to-dry moisture gradient are used for nesting by Wood Thrushes: cove hardwood (69,369 ha), mixed mesic hardwood (33,097 ha), tulip poplar (5033 ha), mesic oak (21,327 ha), xeric oak (20,793 ha), pine-oak (5067 ha), and pine (23,168 ha).

Census Protocol

We conducted 2783 point-count censuses during May and June 1996 and 1997 using the variable circular plot, 10-minute point-count method (Reynolds et al. 1980). We recorded distances to each bird seen or heard during the count period on standardized data sheets and acquired a differentially corrected global positioning system (GPS) location at 2105 survey points. In 1997, all observers used laser range finders to calibrate their distance estimates. Following the recommendations of Ralph et al. (1995), we conducted censuses from dawn to 1015 hours, we spaced census points a minimum of 250 m apart, and we conducted standardized training and testing of all observers prior to the initiation of fieldwork each season.

Productivity Estimates

We searched for nests at four study sites distributed across the northeast quadrant of the park (park headquarters to the Deep Creek Campground) from early May to late June 1992–1997. A total of 426 active nests were monitored following the protocols recommended by Martin and Geupel (1993). Once nests were discovered, they were visited approximately every 3 days until they failed or all chicks were fledged. A chick was assumed to have fledged if it survived in the nest at least 10 full days after hatching. Disturbance and visits to nests were minimized to avoid making the nest more conspicuous to predators.

Nesting success was calculated according to the methods outlined by Mayfield (1975) and Robinson (1988). We estimated total annual fecundity for the population using the model of Pease and Grzybowski (1995). The model assumes a nesting season of 90 days, a 25-day incubation and nestling period (Roth et al. 1996), a daily nest survival rate of 0.958 (our measurement), and a renesting interval of 8 days after a failed nest and 14 days after a successful nest (Roth et al. 1996; Farnsworth 1998). We modified the Pease and Grzybowski (1995) model slightly to incorporate the seasonal decline in clutch size that we and others (Roth et al. 1996) have observed. To do this, we divided the 90-day breeding season into two 45-day intervals, derived fecundity estimates for each interval, and summed these to obtain our annual fecundity estimate. We assumed, based on observations of radio-marked females, that females would renest following successful or failed nesting attempts if there was enough time remaining in the season for a complete nesting cycle.

Habitat Model

We developed a logistic regression model to estimate the probability of detecting a Wood Thrush at any location in the park. The model used Wood Thrush presence or absence at survey points as the dependent variable (2105 survey points for which GPS data were available) and 11 habitat and topographic themes from the park's geographic information system (GIS) as explanatory variables. The GIS information derived for each survey point included 90 m–grid data for vegetation (14 types; MacKenzie 1993); bedrock geology (24 types; King 1968); and five disturbance-history categories ranging from undisturbed sites to sites subjected to industrial logging prior to creation of the park (Pyle 1985, 1988). In addition, eight topographic measures were derived from data from a 30-m digital elevation model (DEM). Topographic measures included slope, aspect, elevation, indices of topographic complexity (Miller 1986), landform (McNab 1989), topographic convergence (Beven & Kirkby 1979), relative moisture (Parker 1982), and relative slope position (Wilds

1996), all of which characterize the shape of the landscape and local moisture regimes at various spatial scales. We used the backwards elimination procedure with $p < 0.1$ (PROC LOGISTIC, SAS Institute 1995) to fit a logistic regression model based on the 11 variables, the squared values of the noncategorical variables, and interactions between the variables. We used concordance as a measure of the model's predictive ability. The percent concordance was calculated by pairwise comparison of every point where Wood Thrushes were present with every point where they were absent. A pair of points was concordant if the predicted probability was higher at points where birds were present than at points where they were absent. We used the ArcInfo (Environmental Systems Research Institute 1998) map algebra language to generate a 90 m–grid probability map based on the parameter estimates from the logistic regression model. The map represents the predicted probability of detecting a Wood Thrush for each grid cell in the park.

Population Estimates

With the program DISTANCE (Laake et al. 1993), we estimated the breeding densities of Wood Thrushes by analyzing the detection distances to birds seen or heard on our point-count censuses. Data were modeled with the hazard detection function, following the recommendations of Buckland et al. (1993).

We used two separate approaches to extrapolate from the point-count density estimates to Wood Thrush population estimates for the entire park. In the first method, we estimated Wood Thrush densities based on 1955 independent points (of which 273 were surveyed in both 1996 and 1997) for each forest community type (cove hardwood, mesic oak, mixed mesic hardwood, tulip poplar, xeric oak, pine-oak, and pine) in which more than five Wood Thrushes were detected; a minimum of five detections were required to make a density estimate. We multiplied the estimated Wood Thrush density within each forest community type by the area of that community type in the park and summed these to obtain a park-wide population estimate. The second method applied density estimates to the probability map generated by the logistic regression analysis. We partitioned the probability map into three zones of detection probability—low, 0–0.25; medium, 0.26–0.50; and high, 0.51–1.0—and calculated the Wood Thrush density within each zone. We multiplied these densities by the area within each zone to generate a total population estimate for Wood Thrushes breeding in the park.

Source-Sink Estimates

Fecundity and survival rates were estimated from both field data and published values in the literature. Recent published estimates of annual adult survival in Wood Thrushes range from those of Donovan et al. (1995*b*), who assumed 0.67 based on the average values reported in the literature, to Roth et al. (1996), who proposed an annual survival rate for adult females of 0.75 based on long-term return rates. Ricklefs (1997) proposed that ratios of after-second-year to second-year birds can also be used to estimate adult survival rates. In 1995 we caught and aged breeding adult Wood Thrushes using the aging method described by Weinberg and Roth (1994). We used both our estimate of annual adult survival based on the ratio of after-second-year to second-year birds and a range of estimates reported in the literature to calculate population growth rates.

Ricklefs (1973) also demonstrated that juvenile survival rates can be calculated directly from estimates of fecundity and adult survival. Using Ricklefs' (1973) approach, a number of authors (Temple & Cary 1988; Noon & Sauer 1992; Donovan et al. 1995*b*) have concluded that annual survival rates in juvenile songbirds approximate 50% of adult survival. Donovan et al. (1995*b*) assume a juvenile survival rate of 0.31 for Wood Thrushes in Missouri, which is close to the estimate of 0.29 Anders et al. (1997) obtained from the survival rates of 49 fledglings radiotracked through the end of August on the same Missouri study site, and to an estimate of 0.31 by Roth and Johnson (1993) based on long-term field data. We assumed a juvenile survival rate of 0.30 to estimate growth rates in our population.

We calculated equilibrium fecundity, expressed as female offspring per breeding female, as derived by Ricklefs (1973) as the ratio of adult mortality to juvenile survival. This measure is equivalent to the source-sink threshold described by Brawn and Robinson (1996) and Trine (1998).

We used estimates of Wood Thrush detectability from our censuses, data from the Breeding Bird Survey (BBS), and a recent land-cover map to estimate the size of the continental Wood Thrush population. By applying an average detection radius of 200 m to a 50-point BBS route, we estimated that each route samples $50 \times \pi \times (200\ \mathrm{m})^2$, or about 630 ha of potential Wood Thrush habitat. Based on this estimate, we used a GIS to convert the relative abundance map (birds per route) generated from the approximately 1500 BBS routes run annually across the species' breeding range (Sauer et al. 1997; Fig. 1a) into a map of estimated breeding density (pairs per 630 ha). We used the minimum values of 0, 2, 4, 11, and 31 birds per route from the BBS relative abundance categories to generate the density map. We then used Loveland et al.'s (1991) 1 km–resolution land-cover map of the United States to cut out a conservative estimate of available Wood Thrush habitat from the BBS-based density map. From the approximately 3.9 million-km^2 breeding range of the birds, we used only the 1.7 million km^2 of deciduous and mixed deciduous-coniferous forest to compute a population estimate. We did not include other forest types or mixed forest-agriculture habitats in our estimate.

Results

Census Results

Of 100 species recorded on our censuses, the Wood Thrush ranked twentieth in abundance, occurring on about 13% of 2783 points censused in 1996 and 1997 (448 individual birds counted). Birds were well distributed across forest types below 1200 m, predominating in mixed mesic, pine, and cove hardwood forest types. We counted an average of 1.22 Wood Thrushes on points where the species occurred. The effective detection radius (Laake et al. 1993) used to estimate the nesting density of Wood Thrushes ranged from 90.9 m in tulip poplar habitats to 122.5 m in pine-oak habitats. Approximately 75% of our detections occurred within 96.5 m, and 25% were beyond 96.5 m. The maximum recorded detection distance was 225 m.

Productivity Estimates

The daily survival rate at 426 nests monitored from 1992 to 1997 was 0.958, which yields an overall nesting success of about 0.35 (Table 1). Successful nests fledged an average of 3.31 chicks.

Whereas daily nest survival rates from all sites combined held steady at about 0.96, rates at individual study sites varied substantially from year to year (Fig. 2). Comparing annual trends in nesting success at our site on the park boundary (Grassy) with sites in the interior of the park (Cosby and Roaring Fork), we found no evidence of higher rates of nest predation or Brown-headed Cowbird parasitism along forest edges. Only seven instances of cowbird parasitism were observed during our study; there was no significant reduction in fledging success at those nests (14 young fledged from five successful nests; Farnsworth & Simons 1999).

Although daily nest survival rates remained constant over the nesting cycle and the breeding season (Farnsworth & Simons 1999; Farnsworth et al. 2000), clutch size and the number of fledglings per successful nest declined over the breeding season. Nests fledging young during the first half of the breeding season fledged 3.49 (SE = 0.08; $n = 94$) fledglings per successful nest, whereas those fledging young during the second half of the season fledged 2.96 (SE = 0.12; $n = 53$) fledglings per successful nest ($p < 0.01$; t test). Applying these data and our overall daily nest survival rate of 0.958 to the model of Pease and Grzybowski (1995) yielded an annual fecundity estimate of 2.76 fledglings (1.38 female fledglings) per breeding pair per year for this population.

Habitat Model

Eight habitat variables showed strong associations with the presence of Wood Thrushes (Table 2). Elevation was the dominant explanatory topographic variable, reflecting the 1200 m–elevation limit of breeding Wood Thrushes in the park. Both the Shannon-Wiener index of topographic complexity, a fairly fine-scale (150 m) measure, and the coarse-scale (km) landform index were useful in explaining the distribution of Wood Thrushes (Table 2). Two vegetation and two geologic types were also associated with the presence (tulip poplar and great smoky group) and absence (pine-oak and rich butt sandstone) of Wood Thrushes (Table 2). Finally, a small but highly significant negative association was evident between sites that were subject to industrial logging at the turn of the century and the present-day occurrence of Wood Thrushes. Overall model concordance, measured from 126,294 possible pairwise comparisons of habitat cells, was high (89.8%). We used the significant variables from the logistic regression model to produce a map of the predicted probability of detecting Wood Thrushes in the park (Fig. 3).

Population Estimates and Source-Sink Status of Park

Estimates of the size of the park's breeding Wood Thrush population extrapolated solely from the abundance of forest community types (Table 3) were similar to those produced by the logistic regression model (Table 4), which in-

Table 1. Annual reproductive success of nesting Wood Thrushes in Great Smoky Mountains National Park, 1992–1997.

Year	*Active nests*[a]	*Nest days*	*Failed*	*Successful*	*Daily survival (SE)*	*Fledglings/ successful nest (SE)*	*Nesting success*[b]
1992	10	109.0	4	6	0.9633 (0.018)	3.50 (0.224)	0.39
1993	49	648.0	25	23	0.9614 (0.008)	3.61 (0.175)	0.37
1994	78	987.5	39	33	0.9605 (0.006)	3.48 (0.124)	0.37
1995	101	1298.0	49	41	0.9622 (0.005)	3.17 (0.130)	0.38
1996	107	1400.0	66	26	0.9529 (0.006)	3.23 (0.139)	0.30
1997	81	1073.5	46	24	0.9571 (0.006)	3.04 (0.195)	0.33
All years	426	5516.0	229	153	0.9585 (0.003)	3.31 (0.066)	0.35

[a] *The sum of failed and successful nests is less than the total number of nests because the fate of some nests could not be determined. All active nests were used to calculate Mayfield daily survival rates.*
[b] *Calculated from a nesting cycle of 25 days.*

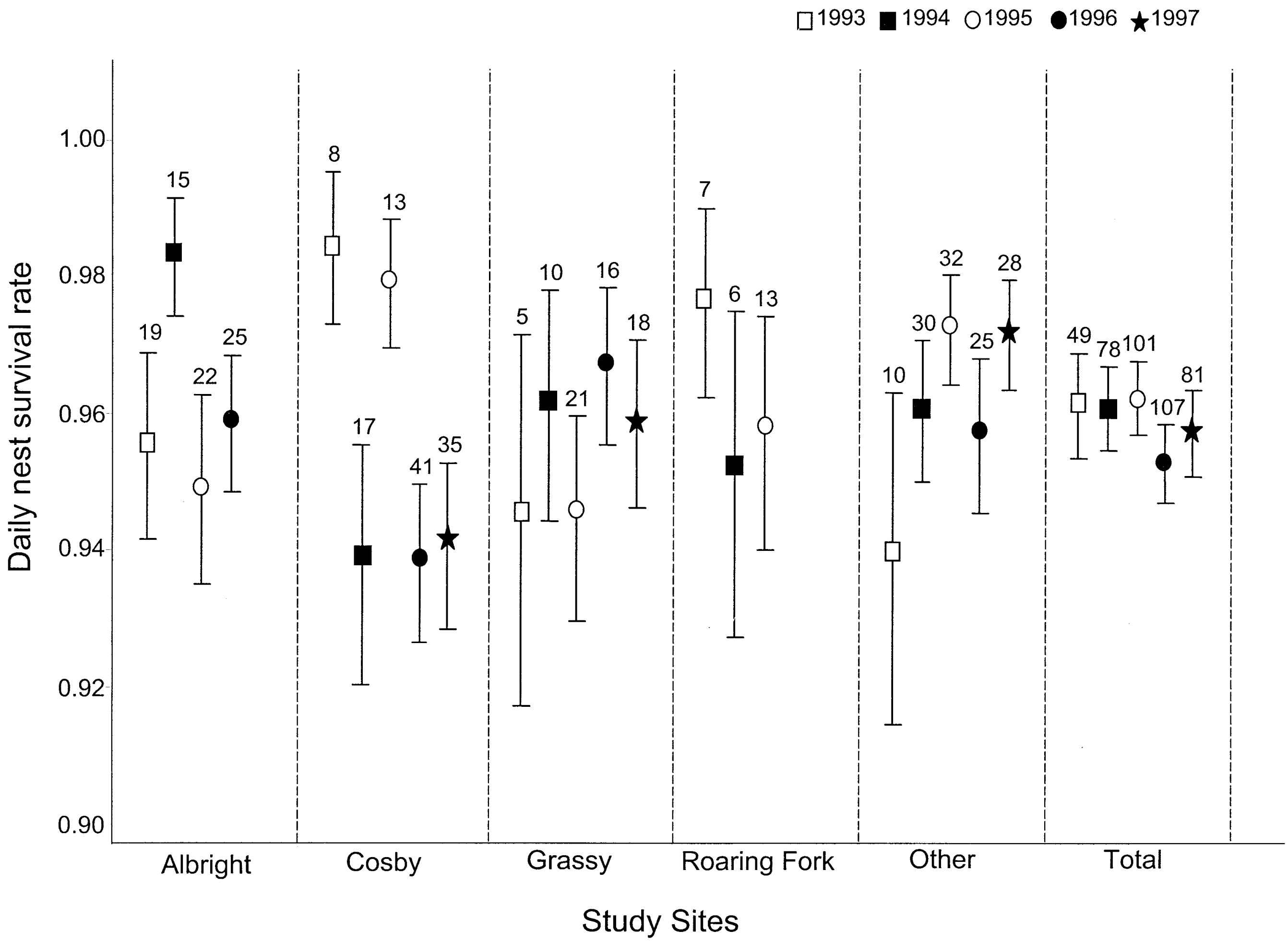

Figure 2. Daily Wood Thrush nest survival rates at study sites in Great Smoky Mountains National Park, 1992–1997. Error bars represent one SE; numbers above bars are number of nests.

corporated many more variables. Both approaches indicate a breeding Wood Thrush population of about 10,000 pairs.

Of 31 adult birds captured in 1995, 23 were after-second-year adults, and 8 were second-year adults. The resulting estimate of adult survival (0.74, SE = 0.08) was within the range found in the literature.

Estimates of annual Wood Thrush productivity derived from our measure of seasonal fecundity (1.38 female young per breeding female per year), a range of three possible adult survival rates, our range of estimated population sizes, and an estimated juvenile survival rate of 0.30 all indicate that Great Smoky Mountains National Park is serving as a population source under all assumptions of adult survival rates (Table 5). Our best estimates of the magnitude of the annual surplus was 2800 females per year. Estimates ranged from 350 to 6630 surplus females per year, depending on the adult survival rate and population size assumed. The estimated minimum size of the continental Wood Thrush population, derived from available habitat and BBS data, was approximately 1.5 million breeding pairs (Table 6).

Discussion

The regional source-sink hypothesis proposes that processes affecting the pattern of forests on the landscape are altering the source-sink dynamics of forest songbird populations. Evaluating this hypothesis with empirical data is not a simple task, given the complex life histories of these birds and the diversity and extent of their breeding habitats. Robinson et al. (1995) demonstrated how large-scale, long-term studies can begin to untangle the complex interactions of habitat conditions and population dynamics. They also identified the need to understand the functional significance of population sources and sinks on the landscape. We attempted to evaluate the role Great Smoky Mountains National Park may play in sustaining forest songbirds at larger spatial scales.

Models that incorporate both habitat and demographic data are useful for investigating these types of questions, but they are inevitably constrained by the limitations of the empirical data available. Our findings suggest that topographic measures may provide useful data

Table 2. Parameters of logistic regression habitat model for Wood Thrushes breeding in Great SmokyMountains National Park, 1996–1997*

Habitat Variables	*Parameter estimate*	*Standardized estimate*	$p > \chi^2$
Intercept	7.190		0.029
Topographic			
elevation	0.036	11.321	< 0.001
elevation × elevation	< −0.001	−5.201	< 0.001
Topographic indices			
topographic complexity	−0.628	−4.851	0.066
topographic complexity × topographic complexity	0.019	4.097	0.029
elevation × topographic complexity	−0.001	−4.637	0.014
landform	0.144	0.872	0.037
elevation × landform	< −0.001	−1.410	0.009
Geology			
rich butt sandstone	−0.943	−0.153	0.020
Great Smoky group	0.565	0.070	0.066
Forest community type			
tulip poplar	0.067	1.427	0.059
pine-oak	−1.660	−1.679	0.013
Historic land use			
industrial logging	−1.280	−0.262	0.009

**Total model concordance was 89.8%.*

for habitat models when accurate vegetation maps are unavailable. Unfortunately, there are no surrogates for good demographic data, which are limited, even for a well-studied species such as the Wood Thrush.

The annual variability of daily nest survival rates among our study sites emphasizes the importance of adequate sample sizes in studies attempting to determine the source or sink status of forest songbird populations

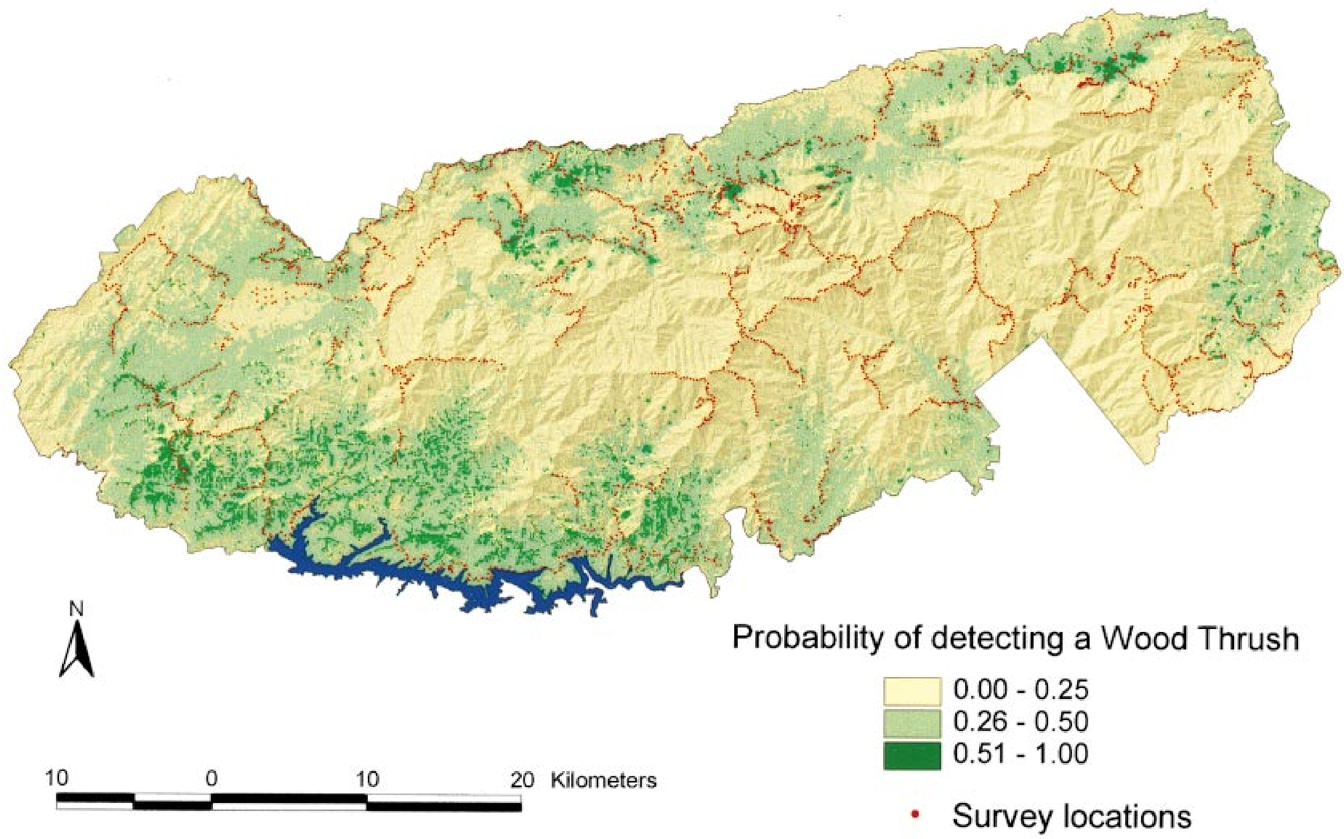

Figure 3. Probability of detecting a Wood Thrush based on parameters of logistic regression model. Darker green shading indicates a higher probability of detecting Wood Thrushes during point count surveys; dots indicate survey points.

Table 3. Breeding Wood Thrush population estimates based on forest community types in Great Smoky Mountains National Park, 1996–1997.

Habitat	*Independent points (total points)*[a]	*No. Wood Thrushes*	*Density pairs/10 ha (CI)*[b]	*Hectares*	*Population estimate (low–high)*
Cove	466 (535)	60	0.33 (0.23–0.49)	69,369	2289 (1595–3399)
Mesic oak	160 (176)	21	0.43 (0.21–0.88)	21,327	917 (448–877)
Mixed mesic	480 (558)	131	0.87 (0.64–1.12)	33,097	2879 (2118–3707)
Tulip poplar	90 (110)	39	1.37 (0.82–2.29)	5514	755 (452–1263)
Xeric oak	299 (331)	48	0.47 (0.31–0.70)	20,793	977 (645–1456)
Pine-oak	91 (98)	15	0.32 (0.15–0.69)	5067	162 (76–350)
Pine	369 (420)	89	0.67 (0.50–0.90)	23,168	1902 (1158–2085)
Total	1955 (2228)	403			9881 (6492–14,137)

[a] *Sample sizes presented as number of independent survey points and total survey points, which include points surveyed in both 1996 and 1997.*
[b] *Density estimates and 95% confidence intervals calculated from program DISTANCE (Laake et al. 1993).*

(Brawn & Robinson 1996; Weinberg & Roth 1998). Our within-site annual estimates of daily nest survival rates (0.938–0.984; Fig. 2) were significantly different, and, if viewed in isolation, would lead to dramatically different conclusions about the status of the park's Wood Thrush populations. Extrapolations from a nest survival rate of 0.984 would characterize the park as a substantial population source, whereas a rate of 0.938 would indicate that the park is a population sink. Anders et al. (1997) reported a similar pattern when comparing productivity data from the same site in Missouri over two time intervals. In contrast, when data were combined within sites and years, we found no significant differences (Farnsworth & Simons 1999).

Our overall Mayfield daily nest survival rates were substantially below those reported in other studies of Wood Thrushes in large forest tracts (Donovan et al. 1995*b*; Hoover et al. 1995; Robinson et al. 1995). Our data suggest that the differences may be the result of higher rates of nest predation at our sites. With the exception of a few nests that may have been blown down during storms, we found no evidence that our nests were failing for reasons other than predation (Farnsworth & Simons 1999). The comparatively high productivity of 3.31 nestlings per successful nest (Brackbill 1958; Longcore & Jones 1969; Donovan et al. 1995*b*; Roth et al. 1996; Trine 1998) suggests that, in the absence of predation, the park provides high-quality nesting habitat for Wood Thrushes. But in spite of the fact that our study area was at least 98% forested, our overall daily nest mortality rate (0.04) was typical of landscapes that are only 20% forested (Robinson et al. 1995). This finding suggests that large, contiguous forests may support a more diverse and abundant predator community (Farnsworth & Simons 2000) than more disturbed or less contiguous sites. Thus, whereas daily nest survival rates may increase with forest patch size at intermediate spatial scales, our data suggest that the inverse relationship between forest patch size and nest predation rates may become nonlinear when patches exceed certain size or disturbance thresholds. This "paradox of nest predation" has been noted on protected areas where predator control has been curtailed (Suarez et al. 1993), but not in other contexts. Tewksbury et al. (1998) found that nest predation rates in western Montana were higher in forested landscapes than in fragmented landscapes and attributed the differences to differences in the predator community. We were also intrigued by our results indicating that Wood Thrush abundance was lower on sites subjected to industrial logging 70 or more years ago. We do not know whether past habitat disturbance currently affects nesting success. Additional research on the ef-

Table 4. Breeding Wood Thrush population estimates based on a probability model derived from land-use, land-cover, and topographic variables in Great Smoky Mountains Park, 1996–1997.

Probability class	*Independent points (total points)*[a]	*No. Wood Thrushes*[b]	*Density pairs/10 ha (CI)*[c]	*Hectares*	*Population estimate (low–high)*
0.00–0.25	1378 (1605)	131	0.26 (0.20–0.35)	131,276	3413 (2626–4595)
0.26–0.50	955 (1075)	226	0.78 (0.62–0.98)	65,566	5114 (4065–6425)
0.51–1.00	90 (103)	40	1.29 (0.83–2.00)	8,823	1138 (732–1765)
Total	2423 (2783)	397			9665 (7423–12,785)

[a] *Sample sizes presented as number of independent survey points and total survey points, which include points surveyed in both 1996 and 1997.*
[b] *Number is less than total detected because only detections within 200 m were used for distance analysis.*
[c] *Density estimates and 95% confidence intervals calculated using program DISTANCE (Laake et al. 1993).*

fects of land-use practices and the predator community on songbird nesting success is warranted.

In spite of higher than expected rates of nest predation, all of the scenarios assumed in our source-sink projections (Table 5) produced evidence that Great Smoky Mountains National Park is serving as a population source. Rates of Brown-headed Cowbird parasitism and nest predation were much lower than those reported from similar studies along forest edges (Brittingham & Temple 1983; Paton 1994). Our estimate of seasonal fecundity is sufficient to produce a population surplus under most conditions. It is similar to the rate obtained by Roth and Johnson (1993) and Weinberg and Roth (1998) from observations of color-marked females. Our best estimate of 2800 surplus females produced per year is substantial from an estimated population of 10,000 breeding pairs. Because we have seen no evidence that Wood Thrush populations are increasing in the park, we assume that most of these birds are dispersing to other areas.

Evaluating the significance of these estimated 2800 surplus females produced per year requires some perspective on the size of the continental Wood Thrush population. Remarkably, this information is unavailable for all but the most endangered passerine birds. The challenges of estimating the size of continental songbird populations are formidable, but we produced a rough approximation for the Wood Thrush by combining our point-count detectability estimates with available habitat and BBS data. The overall detection radius used to estimate Wood Thrush densities on our study sites was 96.5 m. Detection distances are longer in open habitats and shorter in dense habitats, but we believe that the 200-m average detection radius assumed in our analysis is reasonable for most Wood Thrush habitats. Although admittedly rough, our population estimate is conservative because we used a large average detection radius and restricted our analysis to a subset of habitat types. Although the approach is a qualitative first approximation, we hope that it will provide a useful context for our data from Great Smoky Mountains National Park and that it will stimulate much-needed thought, discussion, and research into the source-sink dynamics of forest songbird populations.

Our findings suggest that Great Smoky Mountains National Park, which comprises 0.05% (2057 km^2/ 3.9 million km^2) of the breeding range of the Wood Thrush, contributes surplus annual productivity (Table 5) of at most 6630 surplus females to the estimated continental breeding population. Assuming that 30% of these surplus birds survive to breed, and that they disperse out of the park and nest at densities comparable to those found in the park (one pair per 20 ha), we estimate that the park could be sustaining breeding Wood Thrushes on 398 km^2 of habitat beyond its boundaries. Thus, the maximum extent of the park's influence on the surrounding landscape as a population source would be 0.19 times its area (398/2057 km^2), substantially less than theory suggests may be possible for species with different life histories (Pulliam 1988).

When we began this study, we expected that the relatively pristine forest habitats in the park, embedded within what is still a mostly forested southern Appalachian landscape, would be functioning to sustain Wood Thrush populations throughout the region, and perhaps beyond. Given the dramatic population sinks reported in small forest fragments, particularly in agricultural landscapes (Robinson et al. 1995), we anticipated that equivalently dramatic source areas should exist in unfragmented forests.

Great Smoky Mountains National Park is clearly functioning as a substantial local population source for Wood Thrushes. Wood Thrush productivity in the park is high, and it appears that the park is helping to sustain Wood Thrush populations across the southern Appalachians. Despite the fact that the park has been protected for over 60 years, that it protects one of the largest tracts of wilderness in the eastern United States, and that it lies near the center of the largest contiguous block of deciduous forest in the eastern United States, its potential to sustain Wood Thrush populations over a significantly larger geographic area appears limited. Individual pro-

Table 5. Estimated significance of Great Smoky Mountains National Park as a population source for Wood Thrushes.

Adult survival	*Juvenile survival*	*Equilibrium fecundity*[a]	*Surplus fecundity*[a]	*Population surplus*[a,b] *(low–high*[c]*)*
0.60	0.30	1.33	0.05	500 (350–650)
0.67	0.30	1.10	0.28	2800 (1960–3640)
0.74	0.30	0.87	0.51	5100 (3570–6630)

[a] *Female offspring produced per breeding female per year.*
[b] *Assumes annual fecundity of 1.38 female offspring per breeding female and a current population of 10,000 breeding pairs.*
[c] *Assumes annual fecundity of 1.38 female offspring per breeding female and a current population of 7000 breeding pairs for low estimate and 13,000 breeding pairs for high estimate.*

Table 6. Estimated minimum size of the continental Wood Thrush population.

Relative abundance[a]	*Density (pairs/10 ha)*[b]	*Habitat area (ha)*[c]	*Population estimate*
0	0	32,523,613	0
2	0.03175	35,448,778	112,536
4	0.06349	50,617,417	321,380
11	0.17460	52,426,797	915,389
31	0.49206	2,729,149	134,291
Total		173,745,754	1,483,596

[a] *Minimum value of birds per Breeding Bird Survey (BBS) route (Sauer et al. 1997; Fig. 1a).*
[b] *Based on assumption that each BBS route samples 630 ha of available habitat.*
[c] *Includes only deciduous and mixed deciduous-conifer habitats (1.7 million km^2) from total breeding range of 3.9 million km^2.*

tected areas, even those as large as Great Smoky Mountains National Park, can make only a small contribution to sustaining continental populations of forest songbirds such as the Wood Thrush. Naturally high rates of nest predation, moderate population growth rates, and low nesting densities ensure that relatively small areas of habitat simply cannot sustain populations at significantly larger spatial scales. Although Great Smoky Mountains National Park appears to be serving as a strong local population source, we know little about patterns of dispersal and juvenile survival in this species, or about the status of Wood Thrushes on national forest and private lands surrounding the national park. Our results support the conclusions of others (Donovan et al. 1995*b*; Robinson et al. 1995) that the preservation of many large areas of source habitat must be part of a comprehensive conservation strategy for forest songbirds.

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